3-2010

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Recommended Citation
Carlson, J. M. & Reinke, K. S. (2010). Spatial attention-related modulation of the N170 by backward masked fearful faces. Brain and Cognition, 73(1), 20-7. DOI:10.1016/j.bandc.2010.01.007

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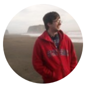
Article *in* Brain and Cognition · March 2010

DOI: 10.1016/j.bandc.2010.01.007 · Source: PubMed



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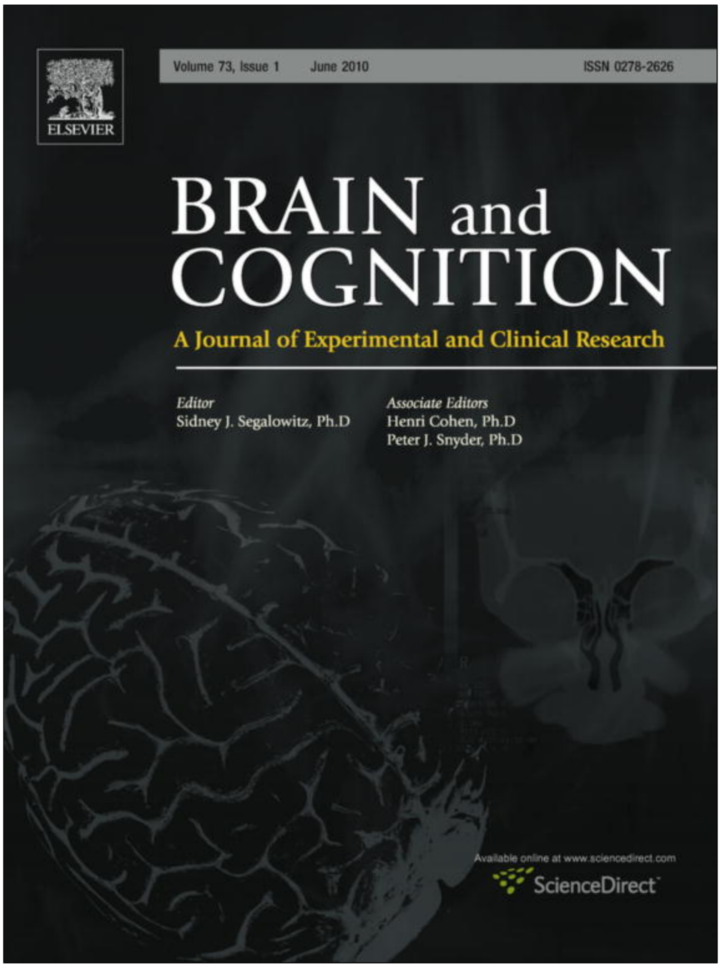
ELSEVIER
Volume 73, Issue 1 June 2010 ISSN 0278-2626
BRAIN and COGNITION
A Journal of Experimental and Clinical Research
Editor
Sidney J. Segalowitz, Ph.D
Associate Editors
Henri Cohen, Ph.D
Peter J. Snyder, Ph.D
Available online at www.sciencedirect.com
ScienceDirect

Brain and Cognition 73 (2010) 20–27

Contents lists available at ScienceDirect

Brain and Cognition

journal homepage: www.elsevier.com/locate/b&c

Spatial attention-related modulation of the N170 by backward masked fearful faces

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ARTICLE INFO

Article history:
Accepted 23 January 2010
Available online 6 March 2010

Keywords:
Facial expressions
Spatial attention
Backward masking
Fear
Emotion

ABSTRACT

Facial expressions are a basic form of non-verbal communication that convey important social information to others. The relevancy of this information is highlighted by findings that backward masked facial expressions facilitate spatial attention. This attention effect appears to be mediated through a neural network consisting of the amygdala, anterior cingulate, and visual cortex. However, a direct investigation of the neural time course associated with orienting to such stimuli has yet to be performed. In the current investigation, a backward masked fearful face dot-probe task was performed while ERPs were recorded. Reaction time results suggest that spatial attention is captured by backward masked fearful faces and attention is focused at the location of the fear stimulus. Masked right visual field fearful faces enhanced the N170 amplitudes of contralateral occipito-temporal electrodes. The rapid contralateral N170 enhancement was positively correlated with participants' behavioral index of spatial attention. Thus, backward masked fearful face-elicited spatial attention facilitates behavior and modulates the early stage of facial processing reflected by the N170.

1. Introduction

Fearful facial expressions are important non-verbal forms of biological communication that signal potential threat and elicit attention from observers (LeDoux, 1996; Ohman, 2005). Backward masking is a procedure in which an initial stimulus (e.g., a face) is immediately followed by a "masking" stimulus (e.g., a second face). The masking stimulus is thought to interrupt the re-entrant processing of the initial stimulus in sensory cortex and accordingly replace and restrict the initial representation (Enns & Di Lollo, 2000). Thus, backward masking is a method in which stimulus processing can be restricted and is commonly used to assess the sensitivity in which fearful faces influence observers (e.g., Mogg & Bradley, 1999a; Whalen et al., 1998). Dot-probe studies[1] indicate that both unmasked (Mogg & Bradley, 1999b; Pourtois, Grandjean, Sander, & Vuilleumier, 2004) and backward masked (Carlson & Reinke, 2008; Fox, 2002; Mogg & Bradley, 1999a, 2002) threatening (fearful and angry) faces facilitate spatial attention. Recent evidence suggests that masked fearful faces facilitate spatial attention through a neural network consisting of the amygdala, anterior cingulate, and visual cortex (Carlson, Reinke, & Habib, 2009). However, the neural time course in which backward masked fearful face-elicited spatial attention modulates visual cortex has yet to be assessed. Event-related potentials (ERP) provide excellent neurotemporal resolution and are thus a well suited method to address this issue. Therefore, the purpose of this study was to assess the neural time course of backward masked fearful face-elicited spatial attention with ERP at posterior electrode sites.

The N170 is a face-sensitive visually-evoked component with a negative peak amplitude occurring approximately 170 ms (130–190 ms) post-stimulus onset at lateral posterior electrode sites and represents the first reliable ERP indication of facial representations (Bentin, Allison, Puce, & Perez, 1996; Jeffreys, 1989). While the later N2 (200–300 ms) has been modulated by backward masked fearful faces (Liddell, Williams, Rathjen, Shevrin, & Gordon, 2004; Williams et al., 2004), the extent to which fearful facial expressions modulate the N170 is unclear. Some studies report unmasked emotional facial expression-related enhancements in N170 amplitudes (Batty & Taylor, 2003; Blau, Maurer, Tottenham, & McCandliss, 2007; Caharel, Courtay, Bernard, Lalonde, & Rebai, 2005; Krombholz, Schaefer, & Boucsein,

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[1] The typical threat-related dot-probe task begins with a fixation cue presented in the center of the screen. The fixation cue is followed by two images simultaneously presented to each visual field where one image is threat-related and the other is neutral. These images are then followed by a target dot appearing in one visual field or the other. If the initial threat image automatically captures spatial attention (relative to the competing initial neutral image) then threat congruent trials (threatening image is spatially congruent with the target) should produce faster reaction times than incongruent trials. The difference in congruent vs. incongruent reaction times is therefore thought to reflect participants' allocation of spatial attention to the threat location.

0278-2626/$ - see front matter Published by Elsevier Inc.
doi:10.1016/j.bandc.2010.01.007

2007; Leppanen, Kauppinen, Peltola, & Hietanen, 2007) while others do not (Eimer & Holmes, 2007; Holmes, Vuilleumier, & Eimer, 2003; Holmes, Winston, & Eimer, 2005). Blau and colleagues (2007) suggest tasks that allow for fear-related enhancements in attention are more likely to reveal modulations in the N170. Consistent with this view, cued spatial attention to peripheral (Holmes et al., 2003) and central (Eimer, 2000a) faces has been found to increase N170 amplitudes while cued attention away from such faces has been found to decrease N170 amplitudes (Jacques & Rossion, 2007) and delay N170 onset (Eimer, 2000b). Therefore, directed spatial attention to or elicited by fearful/emotional faces appear to increase the amplitude of the N170, rather than emotional processing per se. However, it is unclear if spatial attention elicited by backward masked fearful faces enhances the amplitude of the N170.

Generally covert cueing studies of spatial attention reveal contralateral attention-related effects on the negative peak N1 (150–225 ms) and positive peak P1 (100–140 ms) target-evoked potentials thought to represent modulations in early visual processing at occipital electrode sites (attention enhanced P1 and N1 amplitudes: Di Russo, Martinez, & Hillyard, 2003; Martinez et al., 2001; attention enhanced P1 and diminished N1 amplitudes: Fu, Greenwood, & Parasuraman, 2005; Natale, Marzi, Girelli, Pavone, & Pollmann, 2006). Interestingly, the early (90 ms) target-evoked C1 potential, localized to the primary visual cortex (V1), is generally not affected by attention (Di Russo et al., 2003; Fu et al., 2005; Martinez et al., 2001; but see Poghosyan & Ioannides, 2008 for alternative evidence), but the N1, localized to the same V1 source (in addition to V2, V4, and fusiform gyrus; Di Russo et al., 2003) is enhanced by attention. An ERP study of unmasked fearful face-elicited spatial attention (Pourtois et al., 2004) found target-evoked enhanced P1 amplitudes. This contralateral location specific modulation of early visually-evoked ERPs is thought to represent an increase in the visual signal (e.g., threat image or target) to noise (other/background visual input) ratio (see Luck, Woodman, and Vogel (2000) for discussion). Therefore, it appears that spatial attention is generally enhanced by a feedback mechanism that modulates sensory processing and in the case of fearful faces it would be expected that the face-sensitive N170 should be enhanced by fear-specific feedback projections, potentially mediated by the amygdala (Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004).

Spatial attention can be subdivided into orienting, engagement, and disengagement (Posner, 1980). However, without a baseline to compare congruent and incongruent trials it is unclear which aspect(s) of attention is affected (Carlson & Reinke, 2008; Koster, Crombez, Verschuere, & De Houwer, 2004). Dot-probe and visual cueing studies, which have used baseline conditions, indicate that masked fearful faces initiate a rapid covert orienting of spatial attention (Carlson & Reinke, 2008) while unmasked faces typically delay disengagement from threat (Fox, Russo, Bowles, & Dutton, 2001; Yiend & Mathews, 2001).

The aims of the current study were to explore the modulatory effects of backward masked fearful face-elicited spatial attention on reaction times and the face-sensitive N170 ERP component. Based on previous behavioral results (Carlson & Reinke, 2008; Fox, 2002; Mogg & Bradley, 1999a, 2002) we expected that masked fearful faces would facilitate behavioral measures of spatial attention. Specifically, the orienting of spatial attention was predicted to be enhanced by masked fearful faces (Carlson & Reinke, 2008). Based on evidence discussed above (Blau et al., 2007; Di Russo et al., 2003; Fu et al., 2005; Holmes et al., 2003; Natale et al., 2006) it was predicted that masked fearful faces would enhance the amplitude of the contralateral N170. Finally, correlation analyses were performed to test the hypothesis that the predicted N170 and behavioral effects were related.

2. Method

2.1. Participants

Twelve participants (5 male and 7 female) participated in the study. Participants were recruited with fliers posted on the campus of Southern Illinois University and were compensated for their time. All participants were self-reported right handed individuals between the ages of 18 and 35. Additionally, participants were screened to ensure that they were not regularly taking prescription or recreational drugs in addition to screening for serious neurological or psychological disorders. Participants were provided with informed consent and treated according to the guidelines of the Institutional Review Board.

2.2. Procedure and materials

Four (two male and two female) gray scale facial identities of fearful and neutral faces (Gur et al., 2002) were used as the initial face. A fifth neutral female face from this database was used as the mask. Stimuli were presented on a 60 Hz 16″ computer monitor. As shown in Fig. 1, each trial started with a white fixation cue (+) centered on a black background for 1000 ms. Two face stimuli were simultaneously presented (33 ms) to the left and right of fixation. Facial stimuli subtended approximately $5^\circ \times 7^\circ$ of visual angle and were separated by 14° of visual angle. Consistent with masking procedures from other ERP studies (Liddell et al., 2004; Williams et al., 2004), the initial neutral and fearful faces were instantly masked with a neutral face (100 ms). Masks were offset by 1° of visual angle on the vertical *Y*-axis to reduce apparent motion (Liddell et al., 2005). Shifts on the *X*-axis were not used in order to prevent biasing attention. Immediately after the masks, a target dot was presented in the location of either the left or the right face. The target remained until a response was recorded. Participants' used an Electrical Geodesics Inc. (EGI) response pad with their right hand to indicate the location of the target dot (using their index finger for left and middle finger for right). The fixation cue remained in the center of the screen throughout the entirety of each trial and participants were instructed to always fixate on this cue.

Fearful–fearful (FF) and neutral–neutral (NN) trial types were considered baseline conditions independent of an attentional bias to one face over the other. Directed spatial attention trials consist of one fearful and one neutral face occurring in either the LVF or RVF. These trials were half congruent (target dot and fearful face presented on the same side of the screen) and half incongruent (target dot and fearful face on opposite sides of the screen). Trials were weighted so that there were approximately 428 congruent and 428 incongruent trials counterbalanced for visual field in addition to 428 undirected trials (214 NN and 214 FF). The experiment was divided into 15 blocks with a total of 1284 experimental trials. Participants' were provided with feedback of their average reaction time after each block in order to elicit fast responses and provide task motivation.

2.3. EEG acquisition

The ERP experiment was programmed with E-Prime and linked to Net Station acquisition software, which allowed for flagging the EEG data with the time points in which the initial face occurred. By time locking the EEG data to the presentation of the initial face we were able to examine the ERPs associated with each trial type. Electroencephalographic information was recorded with the EGI 128 electrode Hydro Cel Geodesic Sensor Net. Amp calibrations for gains and zeros were completed prior to each participant's session. The EEG signal was digitized at 250 Hz. All participants'

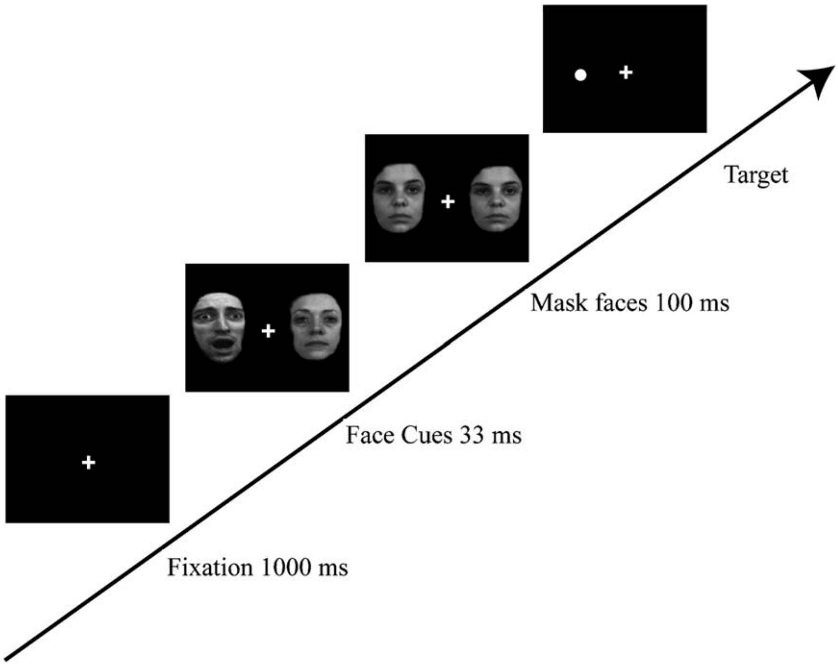

Fig. 1. Each trial of dot-probe task began with a fixation cue appearing in the center of the screen for 1000 ms. Next two faces presented for 33 ms were presented and immediately masked with neutral faces for 100 ms. The target dot then appears on the right or left side of the screen. Depicted is an example of a congruent trial.

impedance levels were kept below 75 kΩ at the beginning of each session.

2.4. ERP data processing

All aspects of EEG data processing were performed with EGI Net Station Waveform Tools. A 0.1 Hz high pass and 100 Hz low pass hardware filter were applied during data acquisition. A 30 Hz low pass filter was applied after data collection in order to eliminate 60 Hz noise-related signal in addition to other high frequency noise. The EEG data was segmented in 800 ms epochs time locked to the onset of the first set of faces with 200 ms pre-stimulus and 600 ms post-stimulus. ERP data underwent an artifact detection process where amplitude deflections of at least 70 μV at eye-blink electrodes (LH: 21, 25, and 127 and RH: 8, 14, and 126, see Fig. 2) were considered eye-blinks and amplitude deflections of 30 μV or greater at eye-movement electrodes (LH: 128 and RH: 125) were considered horizontal eye-movements. This conservative 30 μV criterion for horizontal eye-movements was used to ensure that any differential ERP effects were not due to shifts in overt attention (eye movements), but rather covert attention. Segments containing eye-blinks or eye movements were excluded from data analysis. Additionally, segments with more than 10 bad channels were discarded. Channels were considered bad in each segment if the fast average amplitude exceeded 200 μV (this is a weighted running average algorithm within the EGI software where a single data point exceeding threshold would not necessarily be marked as a bad channel, but several beyond threshold data points would be marked as bad), the differential average amplitude exceeded 100 μV, or a channel displayed zero variance. Additionally, channels were considered bad and replaced across segments if they met the abovementioned criteria in more than 20% of segments. Bad channels were replaced with interpolated data using spherical splines from the remaining channels. The ERP segments were then averaged for each participant so that each electrode had a single waveform for each condition. A 100 ms baseline correction was applied and the data was re-referenced from Cz to the average of all 128 electrodes. Peak N170 amplitudes were extracted between 150–190 ms for each participant. This N170 extraction was limited to symmetrical electrode clusters (similar to those used in other N170 studies with an EGI sensor net; e.g., Blau et al., 2007), located at temporal occipital electrode sites (RH: 50, 51, 57, 58, 63, 64 and LH: 101, 97, 100, 96, 99, 95, see Fig. 2).

3. Results

3.1. Reaction time data

Only correct responses occurring between 100–750 ms were included in the analysis of reaction time (RT) data; resulting in 5.9 % of the data respectively, being discarded for incorrect, premature, and delayed responses. A 2 Cued Visual Field (LVF vs. RVF) × 2 congruency (congruent vs. incongruent) repeated measures analysis of variance (ANOVA) was conducted on participants' RTs. There was a significant congruency effect, $F(1, 11) = 41.91$, $p < .001$, $\eta p^2 = 79.$) where congruent (307.65 ms) trials had faster RTs than incongruent (327.05 ms) trials. There were no main ($F(1, 11) < 1$, $\eta p^2 = .003$) or interaction ($F(1, 11) < 1$, $\eta p^2 = .007$) effects of visual field.

FF(316.94 ms) and NN(316.61 ms) RTs did not significantly differ ($t(11) = -.12$) and were therefore combined to form an undirected attention "baseline" for orienting and disengagement comparisons. If reaction times for congruent trials are faster than baseline, this indicates that backward masked fearful faces speeded the orienting of spatial attention. If incongruent reaction times are slower than baseline, this indicates a slow disengagement of spatial attention from backward masked fearful faces and/or a delayed reorienting of attention to the target dot. As depicted in Fig. 3a, a congruent vs. baseline, paired samples *t*-test revealed a significant orienting effect (*mean difference* = −9.13 ms, $t(11) = -5.94$, $p = .001$) whereas a incongruent vs. baseline *t*-test

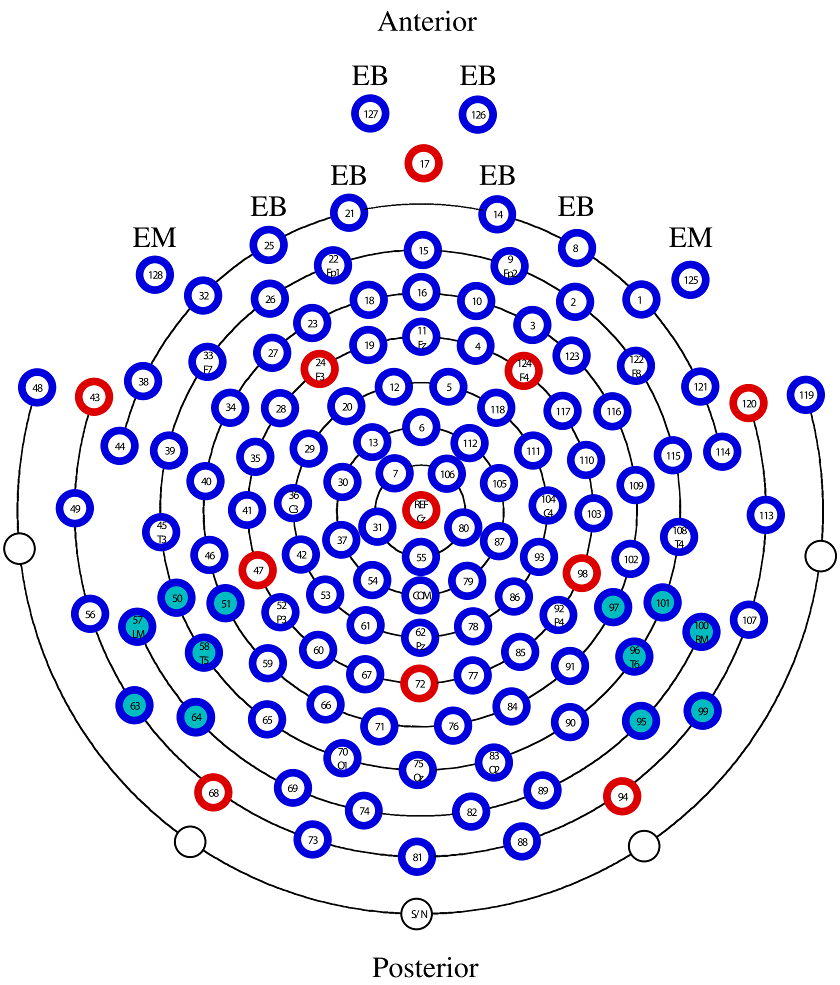

Fig. 2. The EGI 128 electrode Hydro Cel Geodesic Sensor Net is displayed above. Note that channels used for eye-blink (EB) and eye-movement (EM) artifact detection are marked. Additionally, the 12 bilateral occipito-temporal channels used in assessing N170 modulation are shaded.

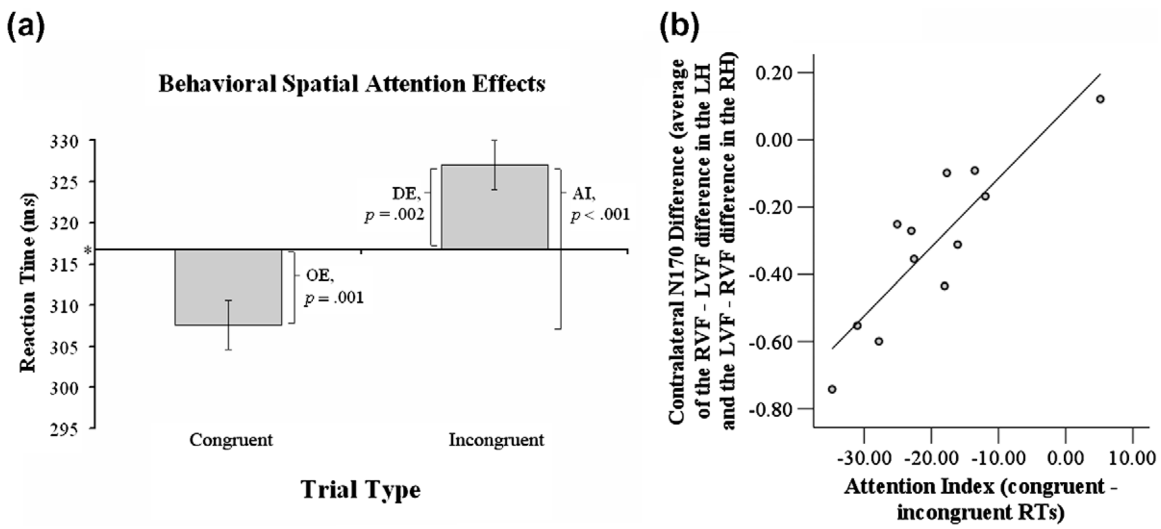

Fig. 3. (a) Reaction times for congruent trials were significantly faster than incongruent trials. This difference represents the overall capture of attention or attention index (AI). A comparison of congruent and baseline trials revealed an enhanced orienting effect (OE) of masked fearful faces. Additionally, incongruent trials were significantly slower than baseline trials indicating there was a slow disengagement effect (DE) from backward masked fearful faces. (b) The contralateral enhancement of the N170 event-related potential at occipito-temporal electrode sites for each participant was highly correlated with their behavioral attention index ($r = .88$). Note that negative N170 differences represent enhanced contralateral amplitudes and negative attention indices represent speeded reaction times for congruent, relative to incongruent, trials. * The X-axis in Fig. 3a is located at the baseline (combined undirected FF and NN trials) reaction time of 316.78 ms.

revealed a significant disengagement effect (*mean difference* = 10.27 ms, $t(11) = 3.95$, $p = .002$).

3.2. ERP data

Artifact detection resulted in 9.38%, 5.85%, and 0.03% of segments discarded for eye blinks, eye movements, and bad channels respectively, which left approximately 181 remaining trials per condition. Similar to previous research with separate facial stimuli presented in a rapid sequence (Jeffreys, 1989), the cue and mask face pairing in each hemisphere elicited bilateral N170s occurring at a single time point (about 185 ms; there were not separate N170s for the initial face and mask). A four-way repeated measures ANOVA assessed the effects of Masked Fearful Face Cued Visual Field (LVF vs. RVF), hemisphere (LH vs. RH), congruency (congruent vs. incongruent), and electrode (1–6) on posterior temporal–occipital N170 amplitudes. As predicted, there was a significant Cued Visual Field × hemisphere interaction on N170 amplitudes, $F(1, 11 = 21.36$, $p = .001$, $\eta p^2 = .66$ (see Fig. 4). Follow up Bonferroni corrected t-tests indicate that the Cued RVF (−2.59 μV) had larger N170 amplitudes than the Cued LVF (−2.07 μV) in the LH ($p_{corr} < .05$). In the RH, Cued LVF (−3.49 μV) N170 amplitudes where larger than those for the RVF (−3.38 μV), but not significantly ($p_{corr} > .05$).

An analysis performed on P1 amplitudes (extracted from the same electrodes sites between 95–135 ms post-stimulus onset) for the Cued Visual Field × hemisphere interaction was not significant ($F(1, 11 = 1.07$, $p > .05$, $\eta p^2 = .09$). An additional analysis of the P1-N170 peak-to-peak differences for the Cued Visual Field × hemisphere interaction was significant ($F(1, 11 = 8.74$, $p < .05$, $\eta p^2 = .44$). Differences between Cued RVF and Cued LVF trials approached significance in the LH (LVF: 4.14 μV, RVF: 4.39 μV, $p_{corr} = .09$) and RH (LVF: 6.62 μV, RVF: 6.40 μV, $p_{corr} = .08$) for P1-N170 differences.

A three-way repeated measures ANOVA assessed the effects of Trial Type (Cued LVF vs. Cued RVF vs. FF vs. NN), Hemisphere (LH vs. RH), and electrode (1–6) on posterior occipito-temporal N170 amplitudes. There was a main effect of trial type ($F(1, 11) = 4.73$, $p < .01$, $\eta p^2 = .30$). Follow up Bonferroni corrected t-tests revealed an marginal effect of fear in undirected attention conditions such that there were larger N170 amplitudes for FF (−3.23 μV), relative to NN (−2.89 μV, $p_{corr} = .07$) trials. Additionally, Cued LVF (−2.75 μV, $p_{corr} = .06$) trials resulted in marginally lower N170 amplitudes than FF trials. There was a trial type × hemisphere interaction ($F(1, 11) = 4.45$, $p = .01$, $\eta p^2 = .29$) where follow up t-tests indicate that in the LH, Cued LVF trials (−2.04 μV) had smaller N170 amplitudes than the Cued RVF (−2.58 μV, $p_{corr} < .05$) and FF (−2.84 μV, $p < .001$) trial types, while the LH difference between Cued LVF and NN trials approached significance (−2.52 μV, $p_{corr} = .12$). Additionally, N170 amplitudes for Cued LVF trials where larger in the RH (−3.47 μV) than LH (−2.04 μV, $p_{corr} < .05$). No other comparisons reached or approached significance.

A correlation between participants' overall contralateral N170 enhancement (average of the RVF–VF difference in the LH and the LVF–RVF difference in the RH) and attention index (congruent–incongruent RTs) indicates that enhanced RTs to fear congruent trials were positively associated with the contralateral enhancement of the N170 ($r = .88$, $p < .001$, see Fig. 3b). That is, larger N170 amplitudes for contralateral relative to ipsilateral masked fearful faces were associated with faster reaction times for congruent compared to incongruent trials (i.e., greater attentional capture). Given that the baseline RT in which orienting and

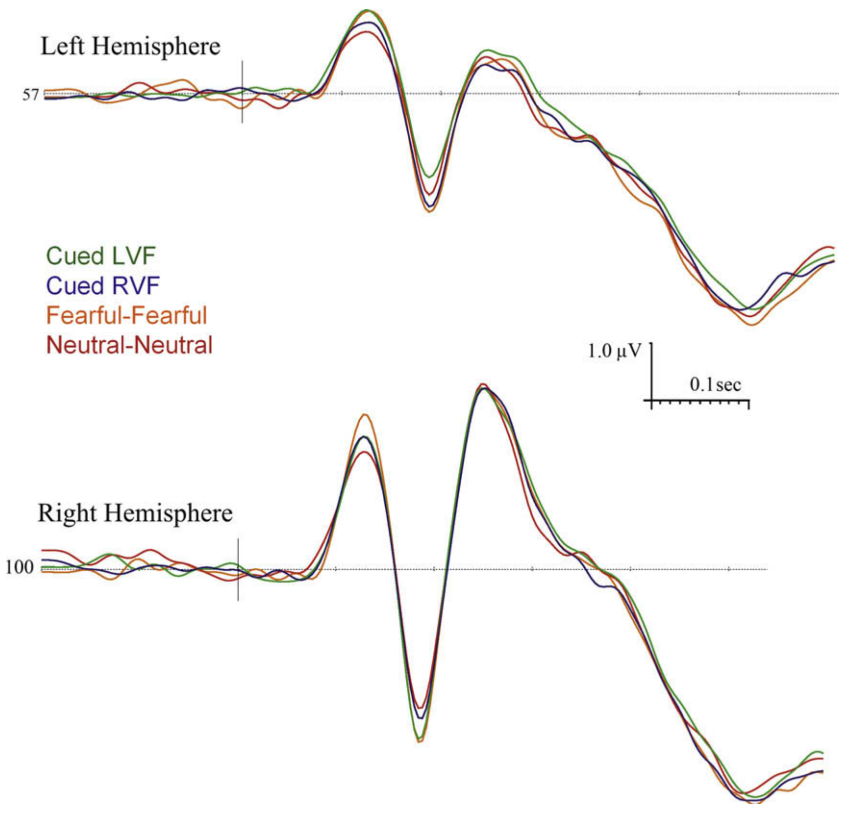

Fig. 4. Depicted are the ERPs for Cued LVF, Cued RVF, Fearful–Fearful, and Neutral–Neutral trial types at representative electrodes in the left (57) and right (100) hemispheres. In the left hemisphere (LH), the Cued RVF had larger N170 amplitudes relative to the Cued LVF. There was a trend, although not reaching significance, for Cued LVF, relative to Cued RVF, N170 amplitudes to be larger in the right hemisphere. Cued LVF trials elicited larger N170 amplitudes in the RH than LH. Additionally, there was a trend for larger P1-N170 peak-to-peak differences for the Cued RVF, relative to Cued LVF, in the LH and larger differences for the Cued LVF, relative to Cued RVF, in the RH. This indicates there may be a small difference between cued visual fields at the level of the P1.

disengagement effects are calculated was between the RTs for congruent and incongruent trials and that the attention index is calculated as the difference between congruent and incongruent RTs, the attention index should therefore capture both orienting and disengagement effects. Thus, an overall measure of spatial attention was correlated with the contralateral N170 enhancement.

4. Discussion

To the best of our knowledge this is the first study to assess the spatial attention-related effects of backward masked fearful faces on the N170. The results are consistent with our hypothesis that masked fearful face-elicited spatial attention enhances the amplitudes of the contralateral N170. In particular, RVF (compared to LVF) fearful faces significantly enhanced the LH N170; however, while the same pattern was observed for LVF fearful faces this contrast failed to reach statistical significance (see Fig. 4). Cued LVF trials elicited larger N170 amplitudes in the RH than LH. Therefore, spatial attention elicited by masked fearful faces modulates the early stage of facial processing reflected by the N170. The behavioral (RT) results add to the existing body of work suggesting that spatial attention is captured by masked fearful faces (Carlson & Reinke, 2008; Fox, 2002) and suggest that this effect is attributed to both speeded orienting and delayed disengagement (Fig. 3a). Finally, the behavioral attention index was found to be highly correlated with the overall contralateral N170 modulation (Fig. 3b). The interpretations of these behavioral and electrophysiological effects are explored below.

4.1. Behavioral spatial attention effects

Previous behavioral research has revealed that *masked* fearful faces facilitate the orienting of spatial attention (Carlson & Reinke, 2008) while other research indicates that *unmasked* fearful faces primarily affect spatial attention by delaying disengagement (Fox et al., 2001; Yiend & Mathews, 2001). Here we provide further evidence that the orienting aspect of spatial attention is facilitated by masked fearful faces and provide novel evidence suggesting that the disengagement (and/or reorienting) of spatial attention is also involved. Unmasked threat stimuli have relatively long stimulus durations, which result in a delayed sampling of attention that may be insensitive to the initial allocation of spatial attention or orienting. Therefore, it is possible that facilitated orienting to unmasked threat occurs at a time point earlier than that typically sampled in studies of unmasked threat. In addition to fearful faces, backward masked angry faces have been shown to facilitate spatial attention (Mogg & Bradley, 1999a, 2002). However, future research is needed to determined which aspect(s) of spatial attention is modulated by masked angry faces (or other emotional faces) and if this effect is reflected on the N170.

4.2. ERP spatial attention effects

While previous research has reported mixed results of emotional facial expressions on the N170 (Batty & Taylor, 2003; Blau et al., 2007; Caharel et al., 2005; Eimer & Holmes, 2007; Holmes et al., 2003, 2005; Krombholz et al., 2007; Leppanen et al., 2007), our results and other research (Eimer, 2000a; Holmes et al., 2003) suggests that directed spatial attention to faces enhances N170 amplitudes. Therefore, the rapid attention grabbing effects of masked fearful faces appear to facilitate visual and facial processing at retinotopically distinct areas of sensory cortex.

The masked fearful face enhancement of the contralateral occipito-temporal N170 may indicate there is a fast fear-based feedback mechanism, which modulates the initial processing of faces and facilitates behavior. This rapid mechanism is consistent with a subcortical route to the amygdala (LeDoux, 1996; Liddell et al., 2005; Morris, Ohman, & Dolan, 1999; Pasley, Mayes, & Schultz, 2004) and an amygdala mediated attention network for orienting to crude threat signals (Carlson et al., 2009). However, it should be noted that the amygdala may be sensitive to a simple facial feature such as the eyes rather than faces per se (Adolphs et al., 2005; Hoffman, Gothard, Schmid, & Logothetis, 2007; Whalen et al., 2004). Subcortical responses are believed to be inhibited by cortical regulation during conscious, but not during nonconscious emotional processing (Jolij & Lamme, 2005). This inhibitory interaction may account for the lack of N170 modulations (Pourtois et al., 2004), behavioral orienting effects (Fox et al., 2001; Yiend & Mathews, 2001), and the relatively late amygdala responses (200 ms, Krolak-Salmon, Henaff, Vighetto, Bertrand, & Mauguiere, 2004) observed in unmasked fearful face studies. However, N170 and orienting effects were found in the current backward masking dot-probe task (also see Carlson & Reinke, 2008 for orienting effects). Thus, enhanced orienting to masked fearful faces may be mediated by an amygdala response eliciting more detailed cortical-based sensory processing, which is reflected in enhanced N170 amplitudes. These effects may be absent in studies of unmasked fearful face processing due to inhibitory cortical regulation (Jolij & Lamme, 2005), which suppresses this subcortical response. On the other hand, the enhanced N170 may reflect a feed forward mechanism in which fearful faces are preferentially processed in the face processing regions of occipito-temporal cortex. Evidence for this possibility is mixed as some ERP studies have reported general emotion related enhancements in the N170 (Batty & Taylor, 2003; Blau et al., 2007; Caharel et al., 2005; Krombholz et al., 2007; Leppanen et al., 2007), while others have not (Eimer & Holmes, 2007; Holmes et al., 2003, 2005). Further research is needed to clarify whether this effect is attributed to a feed forward or backward mechanism.

In either case, the results are consistent with a location specific modulation of the signal (threat) to noise (non-threat) ratio at the occipito-temporal N170. Specifically, we found that RVF, relative to LVF, fearful faces enhanced N170 amplitudes in the LH, but not the RH, which suggests signal was enhanced in the LH relative to the RH. Within the RH the Cued LVF, Cued RVF, NN, and FF trial types all elicited larger N170s and did not significantly differ from each other. This observation could be associated with the RH's relatively greater role in general facial processing, which may preferential engage this hemisphere across trial types. However, only the fearful face cued LVF elicited larger N170s in the RH relative to LH. This RH-LH difference suggests that the fear signal was enhanced in the RH relative to the LH for Cued LVF trials. Therefore, both the Cued LVF and RVF may produce a relative amplification of signal at contralateral occipito-temporal electrode sites; although through different means. Conversely, in undirected attention conditions, FF trials bilaterally enhanced N170 amplitudes (although only marginally) relative to NN trials, which may represent a distributed attentional spotlight. Unlike, the location specific modulation of the N170 in directed spatial attention trials, the distributed spotlight in FF, relative to NN, trials was not accompanied by a facilitation of behavioral responses. The lack of a behavioral facilitation for FF trials may be due to an increase in both signal and noise in this distributed spotlight. Thus, it appears that spatial attention and the facilitation of subsequent location specific behavior are enhanced by a focused spotlight of attention (Posner, 1980).

The spatial attention-related enhancement of the N170 may reflect an enhanced N1 (or early N170) to the neutral face mask that immediately follows the fearful face. This interpretation would be consistent with other unmasked emotional (Pourtois et al., 2004) and non-emotional (Di Russo et al., 2003; Fu et al., 2005; Natale et al., 2006) ERP studies of spatial attention that find enhancements for non-emotional (congruent) targets that follow attention cues. However, unlike unmasked spatial attention paradigms, the first stimulus after the initial fearful face cue (in the current paradigm) is the neutral face mask, not the non-emotional target. Therefore, the current N170 effect may reflect a congruent-like enhancement in the neutral mask face, similar to congruent target effects in unmasked spatial attention studies. Future research should use variable cue-to-mask stimulus onset asynchronies and masks that do not elicit N170 responses to determine if the contralateral modulation of spatial attention is elicited solely by the masked fearful face or the initial face-mask pair. Additionally, while the interaction effect for the peak-to-peak analysis was only marginally significant, the small differences at the level of the P1 may have contributed to the observed contralateral modulation of the N170.

Previous research (Carlson & Reinke, 2008) suggests that the change of expression between the initial fearful face and neutral mask does not account for the behavioral facilitation of spatial attention to backward masked fearful faces. In the current study, we found that the behavioral attention index was highly correlated with the attentional modulation of the N170, which indirectly suggests that the N170 and behavioral effects are commonly attributed to a facilitation of spatial attention by masked fearful faces. However, the effect of the perceptual difference between the initial face and the mask face on ERPs has yet to be directly tested.

Our correlation between the behavioral and electrophysiological indices of spatial attention indicates that these measures are closely linked. Given that the N170 enhancement occurs prior to the speeded reaction times it appears that the contralateral N170 enhancement reflects a neural mechanism in which fearful faces modulate spatial attention and influence subsequent behavior. This contralateral enhancement is location specific and may reflect a modulation of the signal to noise ratio where there is enhanced processing at the specific retinotopic location of the fear stimulus.

In summary, the ERP data indicate that contralateral N170 amplitudes are enhanced by masked RVF fearful faces in the LH while the behavioral data indicate that masked fearful face spatial attention effects are attributable to both rapid orienting and delayed disengagement. Finally, individuals' overall contralateral N170 enhancement predicted the facilitation in RTs associated with directed spatial attention to backward masked fearful faces.

References

Adolphs, R., Gosselin, F., Buchanan, T. W., Tranel, D., Schyns, P., & Damasio, A. R. (2005). A mechanism for impaired fear recognition after amygdala damage. *Nature, 433*(7021), 68–72.

Batty, M., & Taylor, M. J. (2003). Early processing of the six basic facial emotional expressions. *Brain Research and Cognitive Brain Research, 17*(3), 613–620.

Bentin, S., Allison, T., Puce, A., & Perez, E. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience, 8*, 551–565.

Blau, V. C., Maurer, U., Tottenham, N., & McCandliss, B. D. (2007). The face-specific N170 component is modulated by emotional facial expression. *Behavioral Brain Function, 3*, 7.

Caharel, S., Courtay, N., Bernard, C., Lalonde, R., & Rebai, M. (2005). Familiarity and emotional expression influence an early stage of face processing: An electrophysiological study. *Brain and Cognition, 59*(1), 96–100.

Carlson, J. M., & Reinke, K. S. (2008). Masked fearful faces modulate the orienting of covert spatial attention. *Emotion, 8*(4), 522–529.

Carlson, J. M., Reinke, K. S., & Habib, R. (2009). A left amygdala mediated network for rapid orienting to masked fearful faces. *Neuropsychologia, 47*(5), 1386–1389.

Di Russo, F., Martinez, A., & Hillyard, S. A. (2003). Source analysis of event-related cortical activity during visuo-spatial attention. *Cerebral Cortex, 13*(5), 486–499.

Eimer, M. (2000a). Attentional modulations of event-related brain potentials sensitive to faces. *Cognitive Neuropsychology, 17*, 103–116.

Eimer, M. (2000b). Effects of face inversion on the structural encoding and recognition of faces. Evidence from event-related brain potentials. *Brain Research and Cognitive Brain Research, 10*(1–2), 145–158.

Eimer, M., & Holmes, A. (2007). Event-related brain potential correlates of emotional face processing. *Neuropsychologia, 45*(1), 15–31.

Enns, J. T., & Di Lollo, V. (2000). What's new in visual masking? *Trends in Cognitive Sciences, 4*(9), 345–352.

Fox, E. (2002). Processing emotional facial expressions: The role of anxiety and awareness. *Cognition Affect Behavioral Neuroscience, 2*(1), 52–63.

Fox, E., Russo, R., Bowles, R., & Dutton, K. (2001). Do threatening stimuli draw or hold visual attention in subclinical anxiety? *Journal of Experimental Psychology General, 130*(4), 681–700.

Fu, S., Greenwood, P. M., & Parasuraman, R. (2005). Brain mechanisms of involuntary visuospatial attention: An event-related potential study. *Human Brain Mapping, 25*(4), 378–390.

Gur, R. C., Sara, R., Hagendoorn, M., Marom, O., Hughett, P., Macy, L., et al. (2002). A method for obtaining 3-dimensional facial expressions and its standardization for use in neurocognitive studies. *Journal of Neuroscience Methods, 115*(2), 137–143.

Hoffman, K. L., Gothard, K. M., Schmid, M. C., & Logothetis, N. K. (2007). Facial-expression and gaze-selective responses in the monkey amygdala. *Current Biology, 17*(9), 766–772.

Holmes, A., Vuilleumier, P., & Eimer, M. (2003). The processing of emotional facial expression is gated by spatial attention: Evidence from event-related brain potentials. *Brain Research and Cognitive Brain Research, 16*(2), 174–184.

Holmes, A., Winston, J. S., & Eimer, M. (2005). The role of spatial frequency information for ERP components sensitive to faces and emotional facial expression. *Brain Research and Cognitive Brain Research, 25*(2), 508–520.

Jacques, C., & Rossion, B. (2007). Electrophysiological evidence for temporal dissociation between spatial attention and sensory competition during human face processing. *Cerebral Cortex, 17*(5), 1055–1065.

Jeffreys, D. A. (1989). A face-responsive potential recorded from the human scalp. *Experimental Brain Research, 78*(1), 193–202.

Jolij, J., & Lamme, V. A. (2005). Repression of unconscious information by conscious processing: Evidence from affective blindsight induced by transcranial magnetic stimulation. *Proceedings of the National Academy of Sciences of the United States of America, 102*(30), 10747–10751.

Koster, E. H., Crombez, G., Verschuere, B., & De Houwer, J. (2004). Selective attention to threat in the dot probe paradigm: Differentiating vigilance and difficulty to disengage. *Behaviour Research and Therapy, 42*, 1183–1192.

Krolak-Salmon, P., Henaff, M. A., Vighetto, A., Bertrand, O., & Mauguiere, F. (2004). Early amygdala reaction to fear spreading in occipital, temporal, and frontal cortex: A depth electrode ERP study in human. *Neuron, 42*(4), 665–676.

Krombholz, A., Schaefer, F., & Boucsein, W. (2007). Modification of N170 by different emotional expression of schematic faces. *Biological Psychology, 76*(3), 156–162.

LeDoux, J. E. (1996). *The emotional brain the mysterious underpinnings of emotional life*. London: Weidenfeld and Nicholson.

Leppanen, J. M., Kauppinen, P., Peltola, M. J., & Hietanen, J. K. (2007). Differential electrocortical responses to increasing intensities of fearful and happy emotional expressions. *Brain Research, 1166*, 103–109.

Liddell, B. J., Brown, K. J., Kemp, A. H., Barton, M. J., Das, P., Peduto, A., et al. (2005). A direct brainstem–amygdala–cortical 'alarm' system for subliminal signals of fear. *Neuroimage, 24*(1), 235–243.

Liddell, B. J., Williams, L. M., Rathjen, J., Shevrin, H., & Gordon, E. (2004). A temporal dissociation of subliminal versus supraliminal fear perception: An event-related potential study. *Journal of Cognitive Neuroscience, 16*(3), 479–486.

Luck, S. J., Woodman, G. F., & Vogel, E. K. (2000). Event-related potential studies of attention. *Trends in Cognitive Science, 4*(11), 432–440.

Martinez, A., DiRusso, F., Anllo-Vento, L., Sereno, M. I., Buxton, R. B., & Hillyard, S. A. (2001). Putting spatial attention on the map: Timing and localization of stimulus selection processes in striate and extrastriate visual areas. *Vision Research, 41*(10–11), 1437–1457.

Mogg, K., & Bradley, B. P. (1999a). Orienting of attention to threatening facial expressions presented under conditions of restricted awareness. *Cognition and Emotion, 13*(6), 713–740.

Mogg, K., & Bradley, B. P. (1999b). Some methodological issues in assessing attentional biases for threatening faces in anxiety: A replication study using a modified version of the probe detection task. *Behaviour Research and Therapy, 37*(6), 595–604.

Mogg, K., & Bradley, B. P. (2002). Selective orienting of attention to masked threat faces in social anxiety. *Behaviour Research and Therapy, 40*(12), 1403–1414.

Morris, J. S., Ohman, A., & Dolan, R. J. (1999). A subcortical pathway to the right amygdala mediating "unseen" fear. *Proceedings of the National Academy of Sciences of the United States of America, 96*(4), 1680–1685.

Natale, E., Marzi, C. A., Girelli, M., Pavone, E. F., & Pollmann, S. (2006). ERP and fMRI correlates of endogenous and exogenous focusing of visual-spatial attention. *European Journal of Neuroscience, 23*(9), 2511–2521.

Ohman, A. (2005). The role of the amygdala in human fear: Automatic detection of threat. *Psychoneuroendocrinology, 30*(10), 953–958.

Pasley, B. N., Mayes, L. C., & Schultz, R. T. (2004). Subcortical discrimination of unperceived objects during binocular rivalry. *Neuron, 42*(1), 163–172.

Poghosyan, V., & Ioannides, A. A. (2008). Attention modulates earliest responses in the primary auditory and visual cortices. *Neuron, 58*(5), 802–813.

Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology, 32*, 3–25.

Pourtois, G., Grandjean, D., Sander, D., & Vuilleumier, P. (2004). Electrophysiological correlates of rapid spatial orienting towards fearful faces. *Cerebral Cortex, 14*(6), 619–633.

Vuilleumier, P., Richardson, M. P., Armony, J. L., Driver, J., & Dolan, R. J. (2004). Distant influences of amygdala lesion on visual cortical activation during emotional face processing. *Nature Neuroscience, 7*(11), 1271–1278.

Whalen, P. J., Kagan, J., Cook, R. G., Davis, F. C., Kim, H., Polis, S., et al. (2004). Human amygdala responsivity to masked fearful eye whites. *Science, 306*(5704), 2061.

Whalen, P. J., Rauch, S. L., Etcoff, N. L., McInerney, S. C., Lee, M. B., & Jenike, M. A. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *Journal of Neuroscience, 18*(1), 411–418.

Williams, L. M., Liddell, B. J., Rathjen, J., Brown, K. J., Gray, J., Phillips, M., et al. (2004). Mapping the time course of nonconscious and conscious perception of fear: An integration of central and peripheral measures. *Human Brain Mapping, 21*(2), 64–74.

Yiend, J., & Mathews, A. (2001). Anxiety and attention to threatening pictures. *Quarterly Journal of Experimental Psychology Section A-Human Experimental Psychology, 54*(3), 665–681.